PHYSIOLOGICAL OBSERVATIONS ON SOME PERENNIAL HERBS.

A. RIMBACH.

(WITH PLATE XIII)

I.

Arisaema Dracontium (L.) Schott.—During winter *Arisaema Dracontium* consists of a stem-tuber, the growing point of which, covered by several scale leaves, lies at about 5^{cm} below the surface of the earth. It is devoid of roots. Early in April the bud begins to elongate upwards, and at the same time from fifteen to thirty roots break out in a ring like zone from the base of the bud (*fig. 4*). They appear almost simultaneously and grow horizontally, radiating in all directions from their point of origin. They are 1 to 1.5^{mm} in diameter throughout their entire extent, and attain a length of more than 20^{cm}. After a time some of them become somewhat transversely wrinkled at the base, because they undergo there a slight longitudinal contraction. At the end of April the scale leaves protrude from the soil. They are tightly appressed to each other and enclose a hollow, in which the foliage leaf develops (*fig. 6*). In the latter the end leaflet is vertically extended, the lateral leaflets are bent downwards, and the blades of all are involutely rolled up. After having reached the surface of the earth, the scale leaves stop their growth, and at the end of April or beginning of May the foliage leaves and inflorescences break out from their coverings and unfold in the air. In the course of May the inflorescence opens. About the same time a second set of roots is formed immediately above the first one (*fig. 5*), but there is a striking difference between the two. The roots of the second set are thicker, about 2.5^{mm} in diameter, and taper towards the end. They grow from their origin vertically downwards or nearly so, and pass over into a horizontal direction only at their thin end

portion. They undergo very soon a considerable longitudinal contraction in the thickened basal portion, which is usually 2 to 4^{cm} long. After having attained a certain intensity, this contraction manifests itself externally by a shriveling of the root surface. I noticed, however, that these roots of the second set are not in all individuals developed in the same degree. In specimens, for instance, which were located at a considerable depth, these roots differed very slightly from those first formed. On the other hand, in individuals which were placed very superficially I found the roots exceptionally thick and exceedingly numerous.

The contraction amounts to about 40 per cent. within the space of 5^{mm} in the swollen basal portion. It diminishes in intensity towards the thin terminal portion, where no contraction at all takes place. The whole contraction of the root amounts to about 15^{mm} or even more, the contractile region having originally an average length of about 5^{cm}. Of these facts I satisfied myself by marking and measuring the roots during their development in the earth. For this purpose the plants were cultivated in specially constructed culture-cases, furnished with lateral windows, which could be removed thus permitting access to the roots. The active contractile tissue is here, as in other roots of similar structure, the cortical parenchyma. The central axis of vascular bundles with the endodermis is passively contracted, and the same holds good for the epidermis and exodermis and one or two layers of parenchyma immediately below the latter. These passive layers of the outer cortex very soon become folded, and form transverse wrinkles. During contraction, which process lasts in the whole root about three or four weeks, the shortening cortical parenchyma cells elongate very much radially. The root, however, does not grow in diameter, but the outermost layers of the active parenchyma after a time collapse and become tangentially compressed by the inner ones, so that finally a rather wide area of crushed cells is found surrounding a few layers of the still turgescent innermost cells. In the endodermis, as well as in the exodermis, there is also a remarkable

result of the root contraction noticed. The radial longitudinal walls of their cells, being quite straight at the beginning, as contraction sets in become marked with wavy foldings. In the endodermis the waves are strongest in that longitudinal band of the wall which corresponds to the well-known dark spot on the cross-section.

As each root is fastened at its tip to the earth and at its base to the tuber, in consequence of the contraction a tension is set up in it, and the root must give way at the point less firmly fixed. As a matter of fact, mostly the base of the root moves towards the tip and pulls the tuber with it. Thus, by the combined action of all the roots, since all in their basal part point steeply downwards and differ but little in direction, the tuber is drawn down into the earth a certain amount every year.

Thus the contractile roots determine to a great extent the position of the tuber. The latter is found sometimes upright, sometimes lying horizontally, not seldom even turned over with the bud directed downwards, so that the leaf-stalks and stems have to make a strong curvature in order to attain an upright position. The situations are largely due either to a uniform or one-sided pull of the roots. I am not able to say with certainty which direction of growth the tuber would take up by itself, and whether its behavior in this respect would be the same under different external conditions. The annual prolongation of the tuber is in larger individuals from 6 to 10^{mm} (*fig. 6*), and if the tendency of growth were always upright, the dragging action of the roots would of course be of essential importance for keeping the growing point in place and preventing its emerging from the earth.

All the roots are furnished with root-hairs, and form later a few branches of the first order in their terminal portion. At the time of the withering of the leaves all the roots die off, and their scars are then found in a ring-like zone on the surface of the tuber (*sc, fig. 4*).

In the axils of the scale leaves lateral buds originate, four or five every year, which persist after the leaves which support

them have disappeared, and are found in the fall of the same year as lateral protuberances upon the fully developed portion of the tuber (*bd*, *fig. 6*). During the next spring they enlarge considerably, and later, as that portion of the tuber on which they are inserted becomes emptied and dies off, they are set free. As a rule, they do not yet develop a leaf and roots in the same year, but remain dormant and sprout only in the second year after that in which their supporting leaves were vegetating. The tuber always contains but one year's growth in a fully developed state.

The leaves and roots perish in July or August, and soon after the berries ripen. During the germination of the seed, which takes place in the following spring, the cotyledon, growing downwards, elongates so much that the growing point of the stem of the seedling is located 8 to 10^{mm} below the seed (*fig. 1*). The upper end of the cotyledon, which remains in the seed, swells up so as to form an ellipsoid sucker, which finally becomes about 5^{mm} long and displaces in part the emptying endosperm. While this is taking place the first foliage leaf sprouts out and penetrates the earth with a knee-like nutation of its stalk (*l*, *fig. 1*). Already the first root of the seedling, reaching 3–5^{cm} in length and 0.75^{mm} in thickness, is a little contractile at its base, although it does not become wrinkled. During the subsequent development the little stem of the seedling swells up, chiefly below the insertion of the cotyledon, forming a little tuber; out of the latter, during the first year, two, or mostly three, seldom four, adventitious roots are formed (*fig. 2*). Each one of these grows longer and thicker than its predecessor, and develops also a longer contractile region. The fourth root, for instance, is usually about 10^{cm} long and 1.5^{mm} thick; its contraction amounts within the space of 5^{mm} to 40 per cent.; its total contraction amounts to about 10^{mm}. I observed in various specimens that by the work of the roots the little tuber was drawn down from 8 to 10^{mm} during the first vegetative period. So we find, at the end of the first period of growth, the terminal bud of the plant from 15 to 20^{mm} deeper than it was located

in the seed before germination (*fig. 3*). In the following years this migration of the plant downwards continues in a similar way. The alternation of roots mentioned above shows itself from the second year onward.

While the occurrence on one and the same plant of two kinds of roots differing in form and function is not very rare, the formation of these at different times, as in Arisaema, has so far been found only in a few species. I have noted the same fact, for instance, in *Allium ursinum* L., *Fritillaria Meleagris* L., *Scilla bifolia* L., and some other monocotyledons.

Arisaema triphyllum (L.) Torr. resembles perfectly *A. Dracontium* in the behavior of the underground organs.

The contraction of the roots seems to play a great part in another American species of Araceæ, in *Spathyema foetida* (L.) Raf. In this plant a stem-tuber is formed, which grows vertically upwards, dying off gradually at its lower end. This tuber attains 10^{cm} in length and 5^{cm} in thickness, and comprises the products of several years. It forms yearly about fifteen roots near its upper end. These grow obliquely downwards, tapering toward the tip, and produce from their thin end portion lateral rootlets of the first and second orders. They live several years, so that about sixty to seventy of them are found in one plant. All the roots are contractile, and apparently prevent the emerging of the tuber from the ground. This has been assumed also by Foerste, who found the seedlings germinating within an inch of the surface of the ground and the top of the root stock several inches below the surface. I found the seeds germinating on the surface of the soil and the growing point of the tuber in several larger specimens at a depth of about 10^{cm}.

Just the same phenomenon may be observed in *Hypoxis hirsuta* (L.) Coville. This plant also has an upright growing stem-tuber attaining 3^{cm} in height and 2^{cm} in diamèter. All its roots, which start from it in a ring-like belt, are more or less contractile in their thickened basal portion, which becomes transversely wrinkled, and as they grow steeply downwards they are enabled

to drag the tuber vertically into the ground. I found the growing point of older specimens mostly in a depth of 3^{cm}.

In *Trillium sessile* L. I found most of the roots possessing a strongly contractile swollen basal portion, which soon becomes wrinkled. In this species the tuber very often by the power of the roots is drawn into a horizontal or even downwardly directed position.

Mesadenia tuberosa (Nutt.) Britton, a composite growing on wet places of the prairie, has a stem-tuber about 2^{cm} in length, which yearly grows from 10 to 12^{mm} vertically upwards, while it dies off in the same proportion at its lower end (*fig.* 7). The tuber comprises the products of two years, separated by a constriction. Every new member of the tuber, in May after its formation, sends out about twelve roots, originating in a simple ring. These roots grow obliquely downwards and attain a length of more than 30^{cm}. They are at the beginning about 2^{mm} thick, but grow secondarily in thickness, attaining at least a diameter of $4–5^{mm}$. They exhibit considerable contraction, and pull the stem as much back into the ground as it elongates upwards. The roots seem also to show reserve material. They persist through two vegetative periods and form later numerous long but very thin lateral rootlets, branching sparingly in their turn. There is a vegetative multiplication by lateral buds, which become isolated by the decay of the mother tuber.

The species of *Arisaema*, *Spathyema*, *Hypoxis*, *Trillium*, and *Mesadenia* mentioned above can therefore be classed together in one group, characterized by possessing a rhizome growing more or less vertically upward, which becomes drawn down by contractile adventitious roots. To the same group belong also the following species: *Hyacinthus candicans* Baker, *Lilium Martagon* L., *Allium ursinum* L., *Succisa pratensis* Moench, and *Plantago major* L.

II.

Erythronium albidum Nutt.—During summer the bulb of *Erythronium albidum* lies hidden in the earth without aerial organs and without roots. I found the growing point of flowering bulbs,

of which I examined about twenty-five specimens in the month of April, mostly between 15 and 16^{cm} distant from the surface of the earth, the extreme cases being 11 and 20^{cm}. The sterile specimens, the bulb of which as a rule is smaller, were encountered always at a less depth. Of the about 200 specimens of this latter kind which I examined, the larger ones were found at an average depth of 9.5^{cm}, the extremes being 5 and 15^{cm}, and the smaller ones at an average depth of 7.5^{cm}, the extremes being 4 and 13^{cm}. I took into consideration only those individuals which were found on an even ground and apparently had not suffered any considerable disturbance. Hence the smaller plants, as a rule, are found in a more shallow position than the larger ones.

In the late fall—the exact time I am unable to give—the roots break out from the stem portion of the bulb. They appear all at once, their number being in the smallest specimens from four to ten, in the largest from twenty to forty. They are about 0.75^{mm} thick, uniform throughout, become about 15^{cm} in length, and never branch. In the specimens I examined root hairs were not present. These roots do not exhibit any contraction. Their direction of growth varies very much, and seems to be largely influenced by local factors.

At the beginning of April the leaves emerge from the ground, penetrating the earth with the cartilaginous point of the erect inwardly convolute blade. The young specimens develop only one leaf, the older ones a stem with two leaves and with or without a flower. With the development of the aerial organs the emptying of the old bulb-scales and the formation of a new bulb begin. The new bulb may be formed close to the old one, or may be removed from it to a more considerable distance by means of a runner. Of 200 sterile individuals I examined, 114 had formed a runner, the rest not, and of 25 flowering individuals only three had formed runners.

The runner is solid in its basal half, but in its terminal half it contains a narrow, longitudinal channel, the termination of which on the surface is found usually a little below the middle of its

length on the side opposite the roots. In those sterile specimens which do not form a runner the corresponding opening is found on the same side of the bulb at the base of the foliage leaf, about 5^{mm} from the roots upwards. In both cases the opening leads to a hollow space, near the end of which the new bulb is formed. In the sterile individuals mostly two runners are formed by each bulb, the one being about twice as long as the other and also thicker. The longer runner reaches an average length of about 12^{cm}, with a diameter of 2–3^{mm}, the longest I found being 17^{cm} in length. In flowering specimens I found the runner 3–5^{mm} thick and 8^{cm} long, but I do not know the definite length it may attain. Where the new bulb is formed close to the old one, one finds instead of the smaller runner only a little bud. The smaller runner, as well as the little bud mentioned, may be found sometimes at the right, sometimes at the left side of the main bulb.

Without entering into morphological considerations about the parts of stem and leaves which take part in the formation of these structures, we will consider only their physiological behavior. At the end of April the elongation of the runner stops, and the new bulb enclosed in its point begins to swell up. At this time the old bulb-scales are completely emptied, but starch grains are found in the whole extent of the runner and in large quantity in the new bulb. During May the development of the new bulb is accomplished, and at the end of the month the foliage leaves, the old bulb, and the runner die off, so that at the beginning of June the new bulb is isolated. It remains in a dormant state until the fall of the same year, when the above described cycle recommences.

The difference between those specimens which separate the new bulb from the old one by a long runner, and those which form it close to the old one, lies only in the relative length of the stalk uniting the stout stem-portions of the two bulbs. Those stem-portions in which the leaves are inserted and from which the roots start are rich in vascular bundles, and their remnants may be preserved several years. Sometimes two, three,

or four of them are found still attached to a bulb, indicating the places where the plant had rooted in former years. In case no runner is formed, the bulb advances from 2 to 6^{mm} every year, this being the distance of the points of rooting of the subsequent bulbs. Through the formation of a runner, the distance of the subsequent bulbs amounts to 3 to 10^{cm}, being as a rule somewhat smaller than the length of the runner, as the latter usually is curved.

By the growth of the stalk uniting the subsequent bulbs, whether this stalk be short or long, the plant may suffer a dislocation both in horizontal and vertical direction. In both cases the position of the rhizome is somewhat singular, the side from which the roots are formed being turned upwards, and the side on which the bud arises downwards. Where a short stalk is formed, it is directed obliquely downwards and advances the plant a few millimeters in this direction. Where a runner is developed, it grows horizontally at the beginning, but later turns more or less vertically downwards, thus placing the new bulb several centimeters lower. I found in an examination of about 100 specimens the new bulb of the main runner on an average 4.6^{cm} deeper than the old one, while the bulb of the smaller runner was sunken but half as deep. The extreme cases of sinking observed in the larger runner were 1^{cm} and 10^{cm}, in the smaller one 0^{cm} and 6^{cm}. In full-grown flowering specimens a runner seems to be formed but rarely, as I found in most of them the remnants of several years' growth close to the actual bulb, the plant advancing horizontally about 6^{mm} every year. But the young, small individuals also, even in a rather shallow position, do not form a runner every year. Specimens of this latter kind which I found had formed no runner during three years; others, which had developed a runner this year, had been devoid of it in the preceding year, as was shown by the remnants of the last year's bulb; others, furnished with a runner the present year, seemed to have formed one also in the foregoing year, since not the slightest indication of an old bulb was present in their neighborhood.

I do not know what rule may exist in this alternation or by what factors the formation of a runner may be determined. Nevertheless, from my notes it seems that a shallow position of the plant favors the development of a runner. Probably all the shallow, small individuals are derived from seedlings, germinated near the surface of the soil. Their mode of growth must bring them gradually into the depth of the full-grown individuals. By the yearly duplication of their bulbs a rapid vegetative multiplication takes place.

Erythronium mesachoreum Knerr.—This plant, which resembies *E. albidum* very much, inhabits the open prairie. I found the growing point of the bulb in about twenty-five full-grown individuals which I examined between 9 and 13^{cm} distant from the surface of the earth, the average depth being about 11^{cm}. In this species the small, sterile individuals occupy a more superficial position, being found at a depth of from 3 to 8^{cm}. They apparently have originated from seeds. In the early part of April the formation of the new bulb begins. In the young shallow individuals I always found the new bulb removed from the old one by a runner, but the latter is short, the longest I saw being about 20^{mm} in length, and it grows from the beginning vertically downwards, thus placing the plant every year from 3 to 20^{mm} deeper (*fig. 8*). In this species I never noticed the formation of more than one runner by one bulb. The result of this manner of growth is that the formations of the subsequent years are arranged in a vertical row, and I found, in fact, the remainders of the products of five years located in this way above the living bulb; the leaf of the present year making its way through the long channel formed by all the dead integuments (*fig. 9*). By such a movement of growth the plant finally reaches a depth beyond which it does not advance. I found, indeed, that in the old full-grown individuals, situated at a depth of about 11^{cm}, the bulb grows no longer downwards, but horizontally or nearly so, the new bulb rooting about 4^{mm} laterally from the old one.

The observations on *Erythronium mesachoreum* as well as *E. albidum* were made in the neighborhood of Lincoln, Neb.

So far as the physiological behavior of the rhizome and roots is concerned, *Lilium superbum* and *Medeola Virginiana* agree almost perfectly with *Erythronium.*

Lilium superbum L. has a horizontal rhizome, in which stem and leaves are fleshy, and participate in the same degree in the storing of reserve material. Each year's growth of the rhizome is in full-grown specimens about 4^{cm} long, forming at first a runner-like stem portion beset with a few small fleshy scales, and at last a stout, bulb-like structure with numerous crowded fleshy scales, from the middle of which the aerial stem arises. From the under side of this terminal bulb-like portion of the rhizome, just at the place where the aerial stem originates in June, about ten thin roots grow out horizontally, radiating towards all sides and sparingly forming lateral branches of the first order. They do not exhibit any contractility, and last but one year, the rhizome dying off from behind very quickly. I found the growing point of the rhizome in full grown specimens between 7 and 10^{cm} below the surface of the earth. The plant must reach and keep this depth, as the roots are quite inactive, by the movement of growth of the rhizome itself. This behavior, which some other American species of Lilium seem to share, is entirely different from that of *Lilium Martagon* and other species of the Old World, in which the bulb grows vertically upwards, and is drawn down by strongly contractile roots.

Medeola Virginiana L. has a horizontally creeping tuberous rhizome, representing but one year's growth in the fully-developed state. The hibernating, tuber-shaped, end portion of the rhizome bears about twenty or twenty-five thin, thread-like roots, which attain 15^{cm} in length and produce numerous branches of the first and a few of the second order. These roots are not contractile, and radiate in all directions from the rhizome, meandering very much in their course. On even soil I found the rhizome growing in a depth varying from 1 to 4^{cm}. Also here the movement is due to the rhizome alone, the roots taking no part in it.

The roots of *Erythronium albidum* and *E. mesachoreum*, *Lilium superbum*, and *Medeola Virginiana* have only a nutritive function. They are of no great importance in fixing the plant in the earth, nor do they exert any strain upon the parts from which they start, nor do they store any considerable quantity of reserve material. In contradistinction to those of Arisaema, Spathyema, Trillium, and Hypoxis, we find in these roots but little cortical parenchyma, no compressed cortical cell layers, no wrinkling of the root surface, and a total absence of wavy foldings in the longitudinal walls of their endodermis and exodermis. The species of Erythronium, Lilium, and Medeola above mentioned are representatives of a type of geophilous plants in which the rhizome, by its manner of growth, seeks and keeps a certain depth in the ground, without any help of the roots. *Dentaria bulbifera* L., *Paris quadrifolia* L., *Colchicum autumnale* L., *Orchis mascula* L., and *Platanthera montana* Reichb. f. are species which belong to the same type.

III.

Many perennial herbs develop a long tap root, which becomes more or less thick and fleshy, and filled with reserve material. To this group belong the following species: *Kuhnia eupatorioides* L., *Lacinaria punctata* (Hook.) Kuntze, *Grindelia squarrosa* (Pursh) Dunal, *Nothocaleis cuspidata* (Pursh) Greene, *Kuhnistera candida* (Willd.) Kuntze, *K. purpurea* (Vent.) MacM., *Psoralea esculenta* Pursh, *Astragalus crassicarpus* Nutt., *Peucedanum foeniculaceum* Nutt., *Callirrhoë alceoides* (Michx.) A. Gray, *Delphinium Carolinianum* Walt., *Aquilegia Canadensis* L., *Asclepias tuberosa* L., *Lithospermum angustifolium* Michx., *Physalis longifolia* Nutt., and *Allionia nyctaginea* Michx.

In many of these plants the contractility of the root is an important feature. I have noted this phenomenon in *Allionia nyctaginea*. In seedlings of this plant it can be observed easily that the base of the cotyledons, which at the beginning finds itself above the ground, after some weeks disappears under the surface of the earth. That this is really due to the contraction of the root I satisfied myself by marking the root of young

specimens, grown in a special culture case, from their base with lines of India ink 5^{mm} apart. These 5^{mm} spaces shortened to 4^{mm} each within six weeks, which equals a contraction of 20 per cent. At the same time the uppermost line, that next the root base, moved about 6^{mm} downwards, placing the base of the shoot so much deeper.

Also in *Aquilegia Canadensis* I observed a considerable shortening of the root, which results likewise in drawing down the growing point into the earth. In seedlings of *Aquilegia vulgaris* L. I noticed that the growing point of the stem, which immediately after germination stood 8^{mm} above the ground (*fig. 11*) was found at the end of the first summer, in consequence of the contraction of root and hypocotyl, about 6^{mm} below the surface of the earth (*fig. 12*). The upper lateral roots become bent down during this process in a very characteristic manner, (r^1, *fig. 12*). The transverse wrinkling of the surface in the older roots of Aquilegia and Allionia is due to the same cause, and corresponds to the folding of the roots of Arisaema, Hypoxis, and others.

There can scarcely be any doubt that in *Lithospermum angustifolium*, *Nothocaleis cuspidata*, *Peucedanum foeniculaceum*, *Astragalus crassicarpus*, *Kuhnistera candida*, and *K. purpurea* the root is also contractile, although I have not had the opportunity to measure it directly. This seems to be indicated by the following points: the undulating course of the innermost vascular bundles, the transverse wrinkling of the outer bark, the disturbed position of the upper lateral roots, and finally the position of the growing point below the surface of the earth, in spite of the continual prolongation of the perennial stem-portion towards above. Also in *Kuhnia eupatorioides* and *Grindelia squarrosa* contraction seems to occur, although in a less degree, while in *Lacinaria punctata* it possibly may not exist at all. In pieces of roots of *Lithospermum angustifolium* and *Kuhnia eupatorioides* lying in water, I observed after two days a considerable shortening.

In addition I might say something concerning *Lacinaria squarrosa* (L.) Hill, which, although resembling *L. punctata* very

much in its aerial organs and even in its germination, differs considerably in the development of its underground organs. *Lacinaria squarrosa* has an underground roundish tuber about 3^{cm} high with four lateral swellings, a partition that seems to correspond to the tetrarchic arrangement of the vascular bundle in the primary root. I am not able to say, however, whether the tuber is formed only by the basal portion of the primary root, or whether the hypocotyl also or the stem take part in it. At all events, the terminal portion of the main root does not persist, but is replaced by new lateral roots starting from the tuber. Those roots originate in the older plant in four groups of from five to fifteen situated on the four swellings of the tuber (*fig. 13*). They break out from the tuber all at once in the latter part of April at the time when the first leaves appear. They are white, soft, somewhat thickened in their basal portion to an extent of 2 or 3^{cm}, attaining here a diameter of 2^{mm} and tapering very rapidly to a diameter of only 0.5^{mm}. They grow at the beginning almost vertically downwards, reach about 50^{cm} in length, and form very thin branches of the first and second orders, with numerous long root-hairs. The thickened portion of the root consists at the beginning mostly of soft, thin-walled tissue and is contractile, exhibiting according to my measurements in the culture case a shortening of 6–10 per cent. within a space of 5^{mm}. The whole root probably never shortens more than from 2 to 4^{mm}. The contraction ceases after four or five weeks of growth of the root, and during this time the characteristic wavy foldings in the walls of the endodermis and exodermis make their appearance. Later the root becomes more rigid on account of the development of thick-walled cells in the central axis. At the beginning of October, when the fruits are ripe and the aerial shoots begin to die, the roots perish, and during winter there are no living roots on the plant. In old specimens of *Lacinaria squarrosa* the roots probably cannot produce a movement of the tuber, while in younger plants it possibly might happen. But they help apparently to hold the plant in place by the strain hey exert. This contrivance seems to be useful, since

perennial organs of attachment are wanting, and since the tuber is very superficially iocated and the aerial shoot is relatively high, heavy, and exposed to strong winds.

Physalis longifolia Nutt. does not show any contraction of its long fleshy tap root, but reaches a considerable depth in quite another way. The plumule of the seedling is raised 5 to 10^{mm} above the ground and transforms itself afterwards into a long shoot. The primary root grows vertically downwards, sending out numerous thin lateral rootlets, and becomes subsequently thick, fleshy, and filled with starch. Very soon on its surface adventitious buds appear, some at the upper end at the limit of the hypocotyl, rarely on the hypocotyl itself, others deeper down at a distance of 6 or 8^{cm} from the surface of the earth. At the close of the vegetative period the upper part of the plant dies down, but the root, at least a part of it, with its buds, hibernates, and at the beginning of the next year one or more of the buds, now much deeper than the plumule was, grow out by means of the reserve material stored up in the root. In older specimens I found the root 1^{cm} thick and extending to a depth of more than 50^{cm}.

The seedling of *Asclepias Cornuti* Decne shows a development of root shoots quite similar to that of *Physalis longifolia.*

Delphinium Carolinianum, *Callirrhoë alceoides*, and *Nothocaleis cuspidata* are distinguished by the peculiar phenomenon that in older specimens the root is slit into several longitudinal cords in consequence of the dying off of certain tissue portions. I found the root of Delphinium, for instance, divided into eight cords, forming a circle round a central hollow space and connected above and below. In Nothocaleis the root at a length of 12^{cm} becomes variously pierced and divided into two, three, or four longitudinal cords, each of them about 6^{mm} thick, united lattice-like at different heights. This fission of the root is not caused by simple decay of the older tissue, but is due to a peculiar mode of growth in thickness. The details of the processes concerned deserve closer study. A corresponding phenomenon has been observed and studied by Fost in *Gentiana cruciata* L.,

Corydalis nobilis Pers., *C. ochroleuca* Koch, *Salvia pratensis* L., *Aconitum Lycoctonum* L., and *Sedum Aizoon* L. I observed it in *Scabiosa arvensis* L. and saw a fission into four cords also in the subterranean stem of *Gentiana puberula* Michx.

In addition, I have noticed in *Nothocaleis cuspidata* a daily opening and closing of the flower heads. My observations were made between May 1 and 15, in sunny, moderately warm, windy weather on the prairie near Lincoln, Nebraska, where this plant grows naturally. The heads begin to open at 7 A. M., and are at 9 A. M. fully expanded. They remain so till 3 P. M., at which time they begin to close again. At 4:30 P. M. they are all closed, and they stay so during the night.

All the plants mentioned, furnished with a deep tap root, are confined to the place they occupied when germinating. Besides, they lack vegetative multiplication, their only means of propagation being by seeds. Perennials of this type are exceedingly numerous on the prairie. Nevertheless, other forms occur also, like *Helianthus scaberrimus*, with long, horizontal rhizomes, by means of which they are enabled not only to change their place, but also to multiply vegetatively.

Helianthus scaberrimus Ell., as found in early spring, consists of a subterranean shoot 2 to 4^{cm} long, horizontal or ascending at its end, furnished with about twelve long rigid roots, directed obliquely downwards and forwards. At the end of April the terminal bud of the rhizome leaves out, forming immediately long internodes, the first of which bear scale leaves. In the middle of May, from the stem nodes between the roots and from the axils of the scale leaves above them, six to ten white runners start. These take up a horizontal direction and continue growing till August, attaining a length of from 50 to 100^{cm}. Like the leaves of the aerial stem, the scales of the rhizome are opposite, the youngest ones covering the growing point and protecting it during its way through the earth. The runner is 2 to 3^{mm} thick and consists of about twenty internodes, the longest of which may measure 8^{cm}. The last four or five internodes of the runner are very short, and this stout end-portion at the

middle of September gives rise to new roots, while its terminal bud, having stopped its growth, remains quiescent until next spring. At the middle of November, when the aerial shoot has died down, the runner begins to decay from its base, while the roots have reached a length of about 20^{cm} and are still growing. During winter the runner decays, only its end portion with the roots remaining alive, and the plant assumes again the form in which we find it in the spring.

LINCOLN, NEBRASKA.

BIBLIOGRAPHY.

DE VRIES, H. Ueber die Kontraction der Wurzeln. Landwirtschaftl. Jahrbücher **6**: 927. 1877; **8**: 474. 1879; **9**: 37. 1880.

WARMING, EUG. Om Skudbygning, Overvintring og Foryngelse. Naturhist. Forenings Festskr. Kjöbenhavn 1884.

Ueber perenne Gewächse. (Botan. Centralblatt. **18**: —. 1884.)

FOERSTE, AUG. F. The development of *Symplocarpus foetidus* (L.) Salisb. Bull. Torrey Bot. Club **15**: 154. 1888.

FOST, L. Die Zerklüftungen einiger Rhizome und Wurzeln. Bot. Zeitung **48**: —. 1890.

ARESCHOUG, F. W. C. Beiträge zur Biologie der geophilen Pflanzen. Acta Reg. Soc. Phys. **6**: —. 1896.

RIMBACH, A. Ueber die Lebensweise des *Arum maculatum*. Berichte d. Deutsch. Bot. Ges. **15**: 178. 1897.

Lebensverhältnisse des *Allium ursinum*. *Ibid.* **15**: 248. 1897.

Biologische Beobachtungen an *Colchicum autumnale*. *Ibid.* **15**: 298. 1897.

Die kontractilen Wurzeln und ihre Thätigkeit. Beiträge zur wissenschaftl. Botanik. **2**: 1. 1897.

Das Tiefenwachstum der Rhizome. *Ibid.* **3**: 177. 1898.

Ueber *Lilium Martagon*. Berichte d. Deutsch. Bot. Ges. **16**: 104. 1898.

Beiträge zur Physiologie der Wurzeln. *Ibid.* **17**: 18. 1899.

EXPLANATION OF PLATE XIII.

All figures are drawn from nature, and, with exception of *fig. 10*, are natural size. The horizontal dash-lines indicate the surface of the earth.

FIG. 1. Seedling of *Arisaema Dracontium* still in connection with the seed; *s*, seed; *c*, cotyledon; *l*, first leaf; *r*, first root.

FIG. 2. The same, near the end of the first period of growth, having developed all its roots; *t*, tuber; r', contractile adventitious roots.

FIG. 3. The same, in the resting state after the first period of growth.

FIG 4. Small specimen of *Arisaema Dracontium* in April, forming the first set of roots; r^1, thin roots of the first set; *sc*, scars from the roots of the preceding years.

FIG. 5. A similar specimen, in May, forming the second set of roots; r^1, thin roots of the first set; r^2, thick contractile roots of the second set.

FIG. 6. *Arisaema Dracontium*, leafing out; longitudinal section; *sc*, scars from roots of the preceding years; *sk*, remnants of the skin of tuber portions emptied in former years; *bd*, lateral bud; the shaded part of the tuber is to be emptied this year.

FIG. 7. Tuber of *Mesadenia tuberosa*, in May; longitudinal section; r^1, roots formed in the present year; r^2, roots formed in the preceding year.

FIG. 8. Young descending specimen of *Erythronium mesachoreum* in April, with the runner developed; *b*, bulb; *l*, leaf-stalk; *r*, roots; *R*, runner.

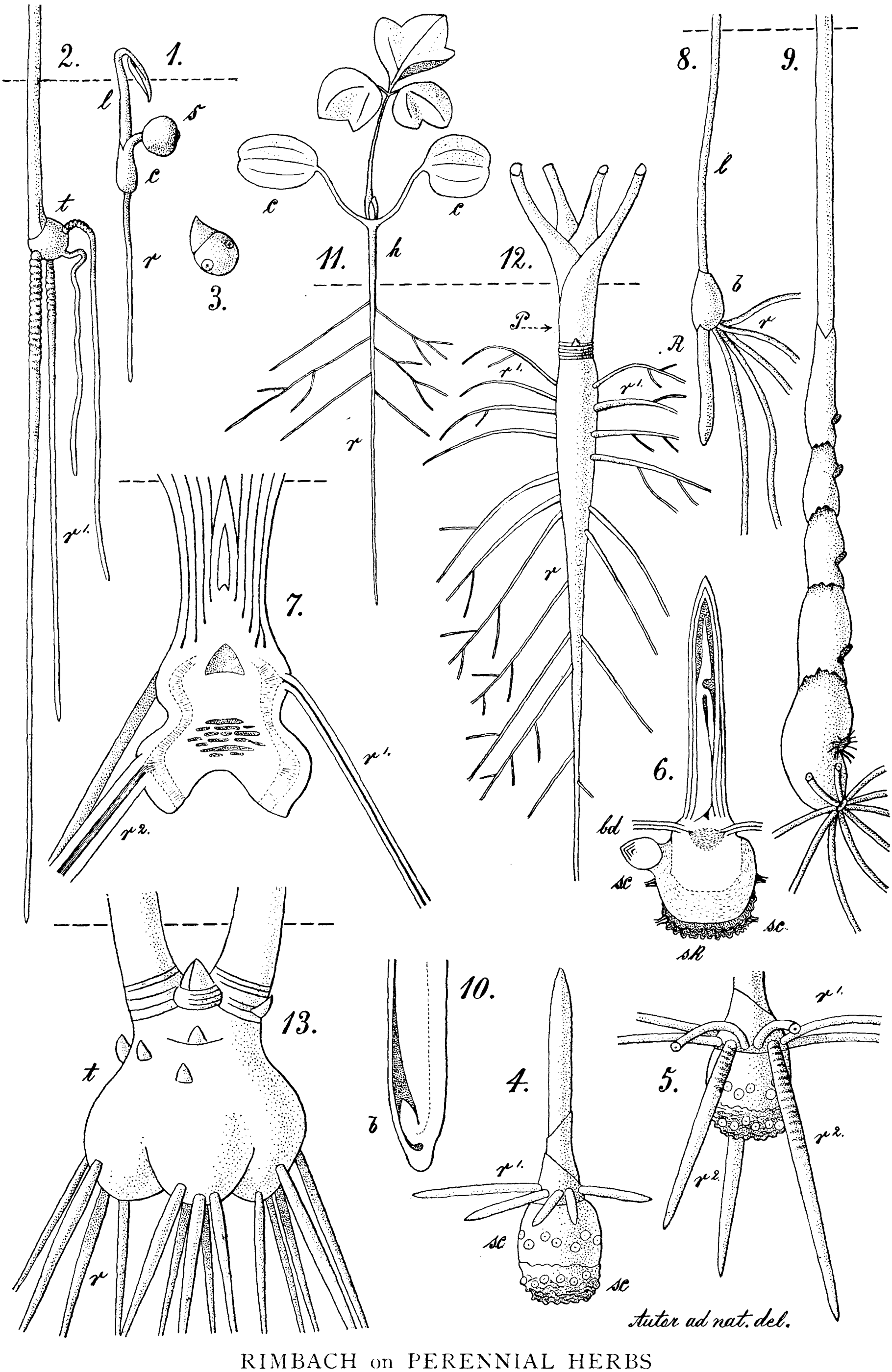
FIG. 9. Young sterile descending specimen of *Erythronium mesachoreum* with its remnants of the five preceding years.

FIG. 10. Tip of the runner of *Erythronium mesachoreum;* median longitudinal section; *b*, new bulb. $\times$ 5.

FIG. 11. Seedling of *Aquilegia vulgaris*, soon after germination; *h*, hypocotyl; *c*, cotyledons; *r*, primary root.

FIG. 12. The same, at the end of the first period of growth; *P*, place where the growing point is situated; *r*, primary root; r^1, lateral roots bent down by the contraction of the main root.

FIG. 13. *Lacinaria squarrosa*, subterranean part of a full-grown specimen in summer; *t*, tuber; *r*, contractile root.



RIMBACH on PERENNIAL HERBS